NEOTROPICAL
BIOLOGY AND CONSERVATION

Neotropical Biology and Conservation
16(3): 397–410 (2021)
doi: 10.3897/neotropical.16.e65875

SHORT COMMUNICATION

New morphological data on the rare sigmodontine *Mindomys hammondi* (Rodentia, Cricetidae), an arboreal oryzomyine from north-western Andean montane forests

Jorge Brito[1], Nicolás Tinoco[2], Jenny Curay[1], Ulyses F. J. Pardiñas[3,1]

1 *Instituto Nacional de Biodiversidad (INABIO), Calle Rumipamba 341 y Av. de Los Shyris. 17-07-8976, Quito, Ecuador*
2 *Sección de Mastozoología, Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador*
3 *Instituto de Diversidad y Evolución Austral (IDEAus-CONICET), Puerto Madryn, Argentina*

Corresponding author: Jorge Brito (jorgeyakuma@yahoo.es)

Academic editor: A. M. Leal-Zanchet | Received 14 March 2021 | Accepted 12 June 2021 | Published 7 July 2021

Citation: Brito J, Tinoco N, Curay J, Pardiñas UFJ (2021) New morphological data on the rare sigmodontine *Mindomys hammondi* (Rodentia, Cricetidae), an arboreal oryzomyine from north-western Andean montane forests. Neotropical Biology and Conservation 16(3): 397–410. https://doi.org/10.3897/neotropical.16.e65875

Abstract

The monotypic rodent *Mindomys* Weksler, Percequillo & Voss, 2006 (Cricetidae, Sigmodontinae) is one of the rarest members of the speciose tribe Oryzomyini. As this species is restricted to the Chocó forests of the western Andean slope in northern Ecuador, our knowledge is based on a few specimens collected decades ago. Here we add the first data on some aspects of external anatomy (cheiridia examined in fresh, ears, rhinarium), genital anatomy (penis), soft anatomy (palate, stomach, caecum) and postcranial skeleton retrieved from a full adult male, recently trapped in Reserva Drácula, Carchi, Ecuador. Several features of this specimen, paradoxically the first to be added to Ecuadorian mammal collections, reinforce the view that *Mindomys* is an arboreal sigmodontine.

Keywords

Chocó, Ecuador, external morphology, Oryzomyini, soft anatomy

Introduction

The tribe Oryzomyini comprises the largest living assemblage of sigmodontine rodents, with a diversity reaching 30 genera (Brito et al. 2020; Percequillo et al. 2021). This remarkable richness, however, encompasses several genera, knowledge of which is limited to basic aspects of craniodental anatomy and external traits evaluated from museum skins. Examples of this are the rare monotypic *Microakodontomys* Hershkovitz, 1993, *Mindomys* Weksler, Percequillo & Voss, 2006 and *Sigmodontomys* J. A. Allen, 1897. In these cases, the addition of a novel specimen can represent a significant input of data (e.g. see *Amphinectomys*; Chiquito and Percequillo 2016). The goal of the present note is to expand the basic anatomical and genetic knowledge of *Mindomys hammondi* (Thomas, 1913), based on a recently secured specimen.

After an extensive small mammal survey involving five years of trapping (a cumulative effort of 1,990 trapping nights, including 990 pit-fall nights) conducted by JB and collaborators at Reserva Drácula (1.006667°S, 78.2247°W, 1067 m alt., Parroquia Chical, Cantón Tulcán, Provincia Carchi, República del Ecuador; geographical coordinates taken by GPS at the trap line), a single specimen referable to *Mindomys* was collected. Obtained from a pit-fall trap set in a dense montane forest in the Chocó Ecoregion (Fig. 1), the animal was preserved as a carcass in skin with the skeleton cleaned and housed at the mammal collection of the Instituto Nacional de Biodiversidad (INABIO, Quito, Ecuador) under the number MECN 6228. It was a male with scrotal testes, an adult according to the wear of the molars (Fig. 2); external and craniodental measurements are provided in Appendix 1.

Figure 1. General landscape (**A**) and fieldwork showing a pit-fall fence (**B**) at Reserva Drácula, Carchi, Ecuador.

Figure 2. Skull (cranium in dorsal, ventral and lateral and mandible in labial view) and right upper and left lower molar series of *Mindomys hammondi* (MECN 6228; Reserva Drácula, Carchi, Ecuador).

Prior to this specimen, *M. hammondi* was known from a small sample of individuals mostly collected at or near its type locality (Mindo, Pichincha, Ecuador; Thomas 1913) during the first half of the past century (Weksler et al. 2006; Tirira and Azurduy Högström 2011; Percequillo 2015). The novel material from Reserva Drácula represents the first data, based on a fresh individual, of several traits related to external and soft anatomy. Here, these features are explored following contributions of Voss (1988), Carleton (1998) and Weksler (2006) for general external anatomy; Brown (1973) and Haidarliu et al. (2012, 2013) for rhinarium topography; Quay (1954) and Carleton (1980) for soft palate morphology; Carleton (1973) for stomach gross morphology; Vorontsov (1967) for caecum anatomy; and Hooper and Musser (1964) for male genital anatomy.

According to Percequillo (2015: 360) in *M. hammondi* "the forefeet are robust and completely covered above by short brown hairs. The hind feet are densely covered by short hairs above that are overall whitish or grayish, but brown basally and white apically. Ungual tufts are short and sparse but extend to the tips of the claws." The MECN 6228 allows improvement of this cheiridia description, based of museum skins. The fore foot has robust and proportionately stocky and short

Figure 3. External morphology of *Mindomys hammondi* (MECN 6228; Reserva Drácula, Carchi, Ecuador): dorsal (**A, C**) and ventral (**B, D**) aspect of right fore foot (**A, B**) and hind foot (**C, D**); left ear in internal view (**E**); and rhinarium and upper lips in frontal view (**F**).

fingers (Fig. 3A, B). Dorsally, the metacarpal region is covered by long, but sparse brown hairs, while the fingers are coated with whitish hairs not concealing the dermal scales. Palmar anatomy involves five fleshy pads; although they are large, an important portion of the palmar surface is not formed by pads, but by squamated skin. In this respect, a significant space is left between the groups of interdigital pads and the palmar pads, suggesting it as one of the main axes to manus flexion. While the pollex is short and bearing a nail, the remaining fingers are roughly subequal in length and terminate in short claws, basally opened and covered by sparse whitish ungual tufts. Each main finger has four or five internal smooth rings and a turgent distal callus. The hind foot resembles the fore foot in dorsal coat, general

Figure 4. External morphology of *Mindomys hammondi* (MECN 6228; Reserva Drácula, Carchi, Ecuador): distal left hind foot, internal view (**A**); base of the tail in dorsal (**B**) and ventral (**C**) view.

finger morphology and ungual tufts development (Fig. 3C, D). The digits are comparatively short; the plantar portion is short and broad, acquiring a subtriangular outline. The interdigital pads are similar in size although pads 2–3 are slightly larger than 1–4; the hypothenar pad is small relative to the total plantar area. The latter is covered by scales surrounding the interdigital pads, but smooth between plantar pads. The inner surfaces of the fingers are basally annulated by scaled rings and distally annulated by smooth rings and terminate in well-developed calluses; short, but acute basally-opened claws tip all digits, including the hallux (Fig. 4A).

Ear and rhinarium morphology have generally not been addressed, except for general aspects (e.g. hairiness), in sigmodontine anatomical studies, probably because both structures are poorly preserved in museum skins. Percequillo (2015: 360) stated for the original series of *M. hammondi* that "both external and internal surfaces of the ears are well furred with short, entirely brown hairs." The specimen MECN 6228 has a rather simple auricular pinna, bean-shaped, easily visible above head fur and with the concha and antitragus scarcely developed. In addition, the internal surface looks almost naked and colourless, being covered towards the margin by delicate sparse whitish hairs (Fig. 3E). In most muroids, the naked rhinarium is frequently overshadowed by haired folds of the muzzle; however, the surroundings of the nostrils and the internarial septum are often free from hair and sometimes offer a variety of morphological traits (Hill and Osman 1948; Brown 1973). The specimen MECN 6228 has a moderately large rhinarium with elongated lateral nostrils slightly dorsally covered by a tuft of hairs; the dorsum (sensu Brown 1973 or regio suprarhinarica, according to Haidarliu et al. 2012) is well-developed and looks pinkish. The nasal tubercles are bulbous and rounded, being crossed transversally

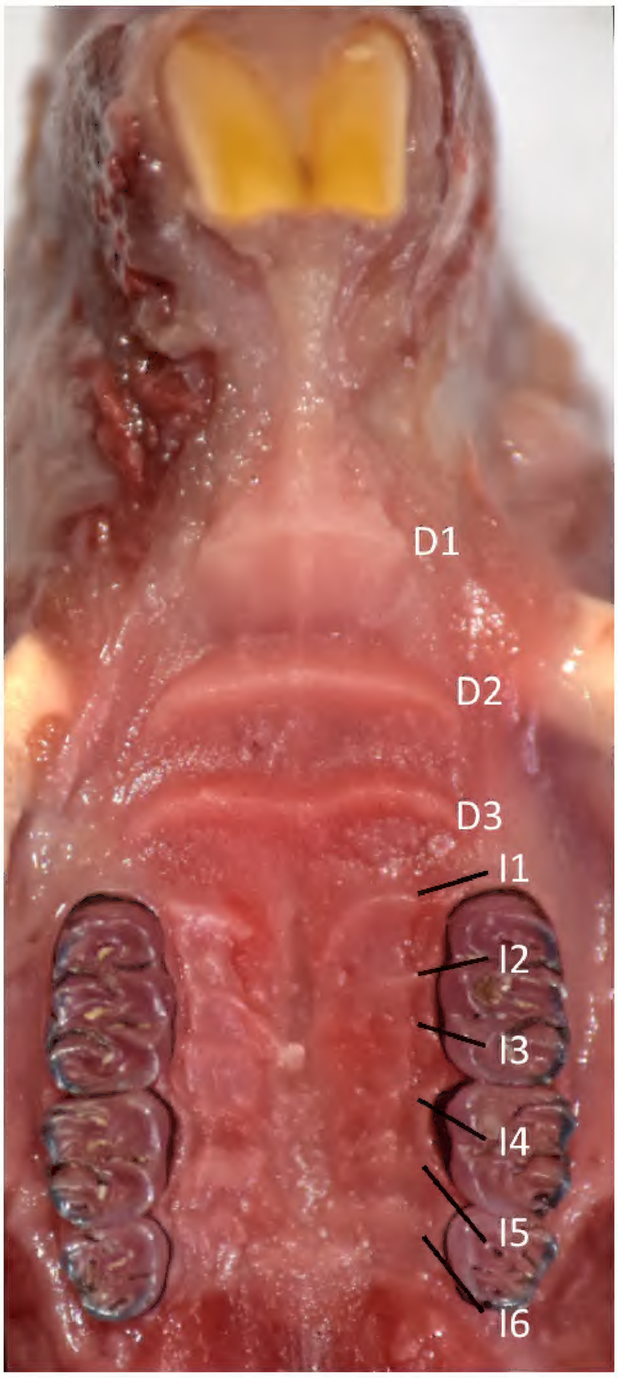

Figure 5. Soft palate morphology of *Mindomys hammondi* (MECN 6228; Reserva Drácula, Carchi, Ecuador). Abbreviations: D1–D3 = diastemal rugae; I1–I6 = interdental rugae.

by three faint grooves, defining the crus superius and crus inferius. Each nostril is basally accompanied by a "pinched" alanasi (Fig. 3F).

Although the tail was described as covered by "long hairs that partially conceal large scales" and "the tail scales and hairs are blackish or dark brown and there is no dorsoventral countershading" (Percequillo 2015: 360), in the MECN 6228, it seems naked. Actually, the tail surface is covered by short and rigid caudal triplets of hair leaving the basal scutelation clearly visible. In addition, at least at the base of the tail, the longest hair of the triplet, the median one, covers two scale rows. The tail scales are hexagonal above and squared below and the dorsoventral countershading is marked (Fig. 4B, C).

According to the studied material, the soft palate has three diastemal (complete) rugae, a condition widespread in cricetids (Carleton 1980). On the contrary, palate (or interdental) rugae are at least six and much lower in relief compared to the interdental folds of other oryzomyines (Fig. 5).

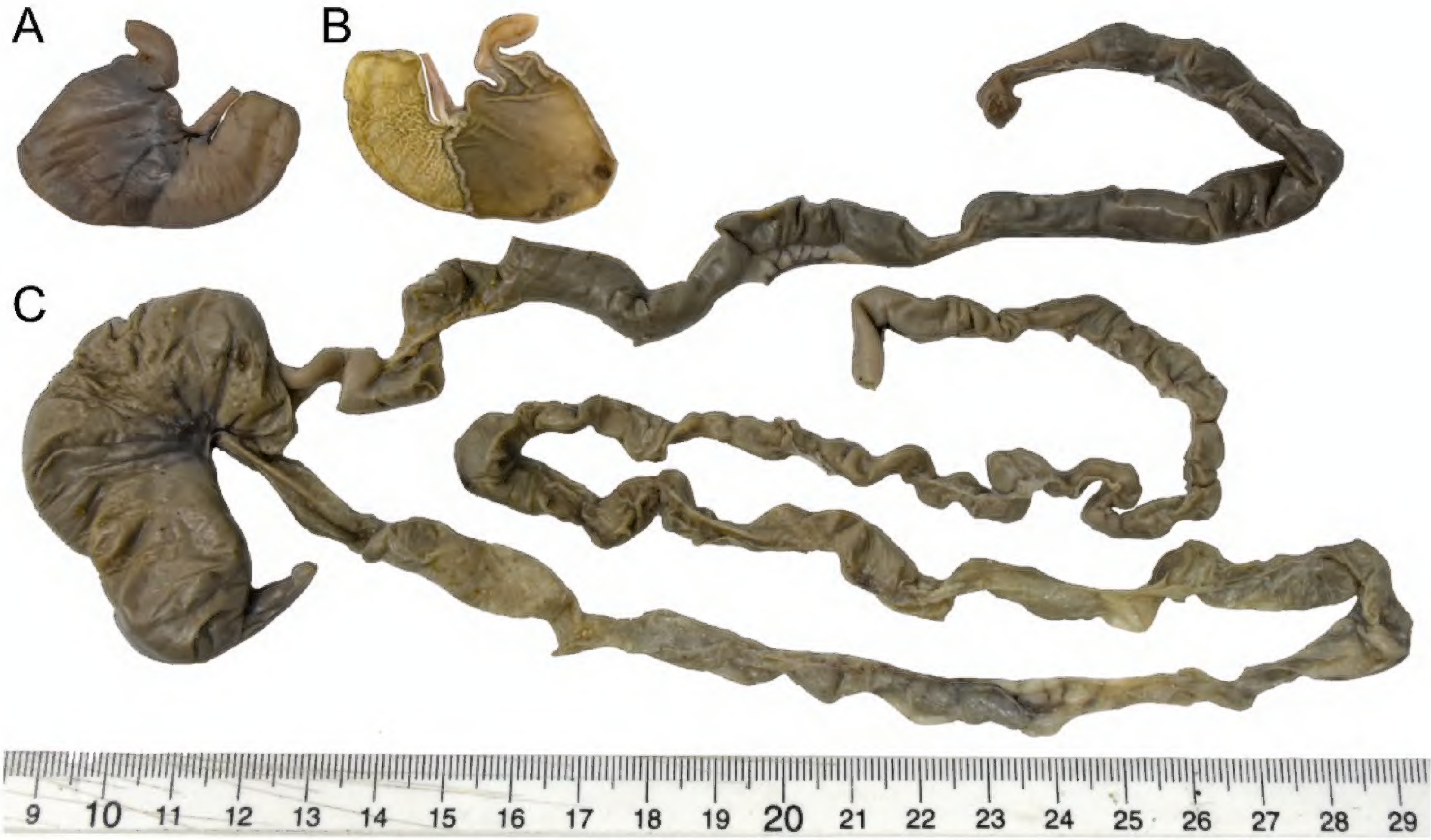

Figure 6. Gross anatomy of partial digestive system of *Mindomys hammondi* (MECN 6228; Reserva Drácula, Carchi, Ecuador): stomach in external (**A**) and internal (**B**) view; and intestine in external view (**C**). Scale in millimetres.

The MECN 6228 revealed no gallbladder; the absence of this organ is a synapomorphy for the tribe (Voss and Carleton 1993). Its stomach fits the unilocular-hemiglandular condition (Fig. 6A, B), also a widespread condition within oryzomyines (Carleton 1973; Weksler 2006). A markedly thick bordering fold bisects the organ in more or less equal-sized halves; in addition, the glandular epithelium scarcely surpasses to the left the level of the oesophageal orifice. The corpus is almost entirely lined by rugged cornified epithelium and the pre-pyloric part is well developed. The incisura angularis is very shallow (Fig. 6B). The pre-caecum intestine accounts for 550 mm, while the post-caecum intestine is about 330 m in length. The caecum is neither haustrate nor sacculate, appearing as a single pouch of about 80 mm in length; its distal portion is produced as a clearly marked appendix (Fig. 6C). Although the entire intestine looks impressive because its length, the single condition of the caecum, plus the uncomplicated colonic region, suggest a moderate digestive efficiency (Björnhag 1994; see Vorontsov 1982 for additional data on oryzomyines).

Regarding its genital morphology, the specimen MECN 6228 showed that the bacular shaft is straight, tapering distally and terminating in a weakly developed head. There is a slight expansion along the medial part of the bony shaft. The base is broad and notched in dorsal and ventral view. The cartilaginous trident is about 40% of the shaft length and the medial digit protrudes slightly beyond the lateral ones (Fig. 7D). The glan penis is large in relation to its diameter with well-defined parotoid lobes and the terminal crater directed distally, its opening bordered by a ring of tissue and lacking spines (Fig. 7A–C).

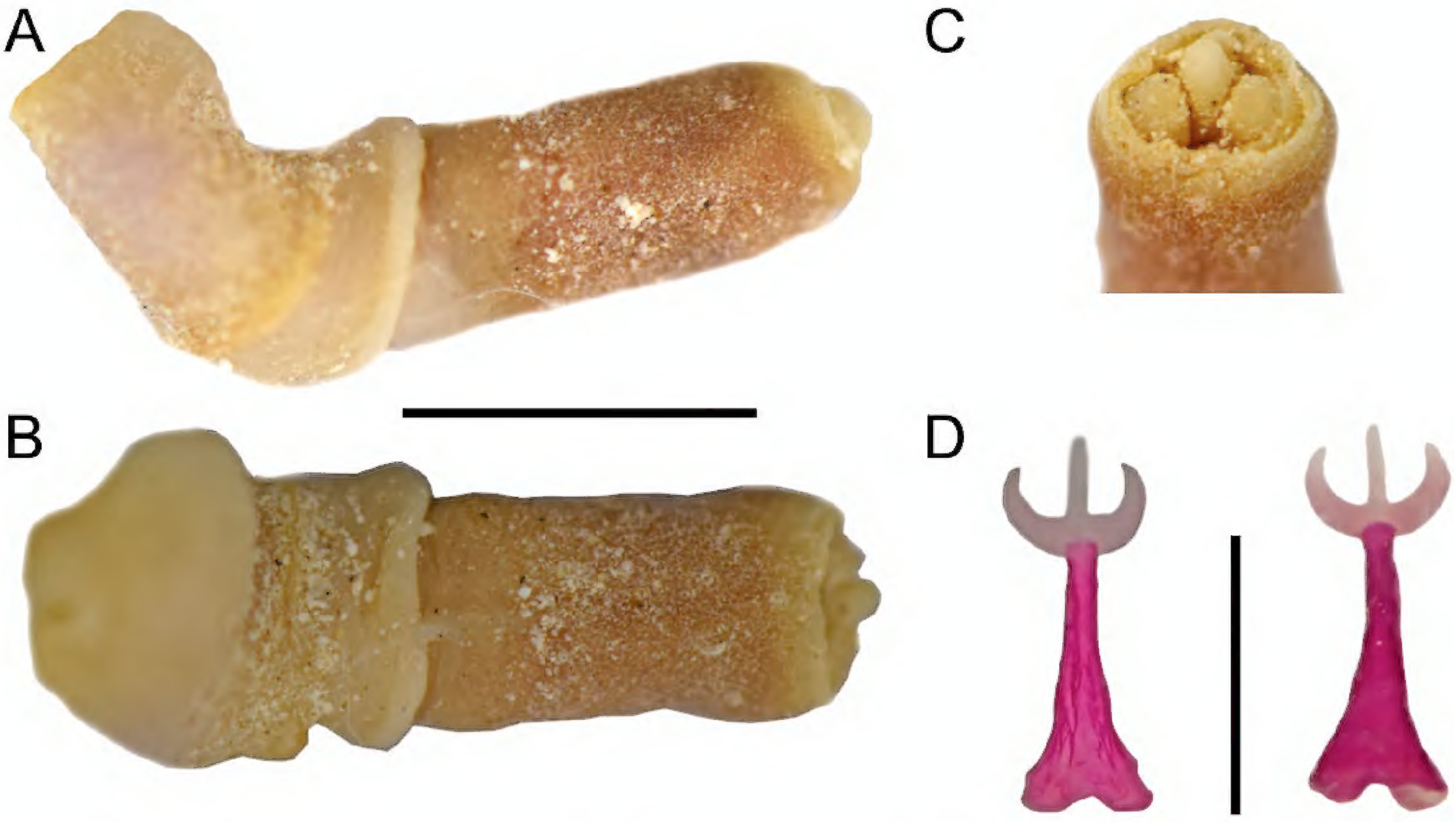

Figure 7. Penis of *Mindomys hammondi* (MECN 6228; Reserva Drácula, Carchi, Ecuador): External morphology of the penis in lateral (**A**), ventral (**B**) and apical (**C**) view; baculum (stained) and cartilaginous trident in dorsal and ventral view (**D**). Scale bars: 5 mm.

There are no previous data about the postcranial skeleton in *Mindomys* (Weksler et al. 2006). The MECN 6228 revealed that the tuberculum of the first rib articulates with the transverse processes of the seventh cervical and first thoracic vertebrae and the second and third thoracic vertebrae have differentially elongated neural spines, with the dorsal end of the second markedly broadened (Fig. 8B). The vertebral column is also composed by 19 thoracicolumbar vertebrae, the 16th with moderately developed anapophyses and the 17th with little-developed anapophyses, along with 4 sacral vertebrae and 35 caudal vertebrae with complete haemal arches only in the first, second and third. *Mindomys* has 12 ribs. The scapular notch extends to half of the scapula and the scapular spine reaches the caudal border (Fig. 8A). A cursory inspection of the main long bones showed the presence of a supratrochlear foramen of the humerus. The tibia in the medial view exhibits a proximal curvature with a sigmoid shape and a well-developed tibial crest. The third trochanter of the femur is barely expanded laterally and reaches the distal half. The contact between the tibia and fibula occurs in the more distal part of these bones and the fibula reaches 65% of the length of the tibia (Fig. 8).

As was noted above with respect to several traits (e.g. ears and tail hairiness, general pes morphology), the MECN 6228 departs partially from the condition described by Percequillo (2015), based on the type series of *M. hammondi* (see also Weksler et al. 2006). We prefer to take these differences as an expression of the almost unexplored intraspecific variability for this taxon. Having said that, the type locality of *M. hammondi*, “Mindo, N.W. of Quito. Alt. 4213 ft.” (Thomas 1913: 570), the provenance of most of the known specimens for the species (Weksler et al. 2006),

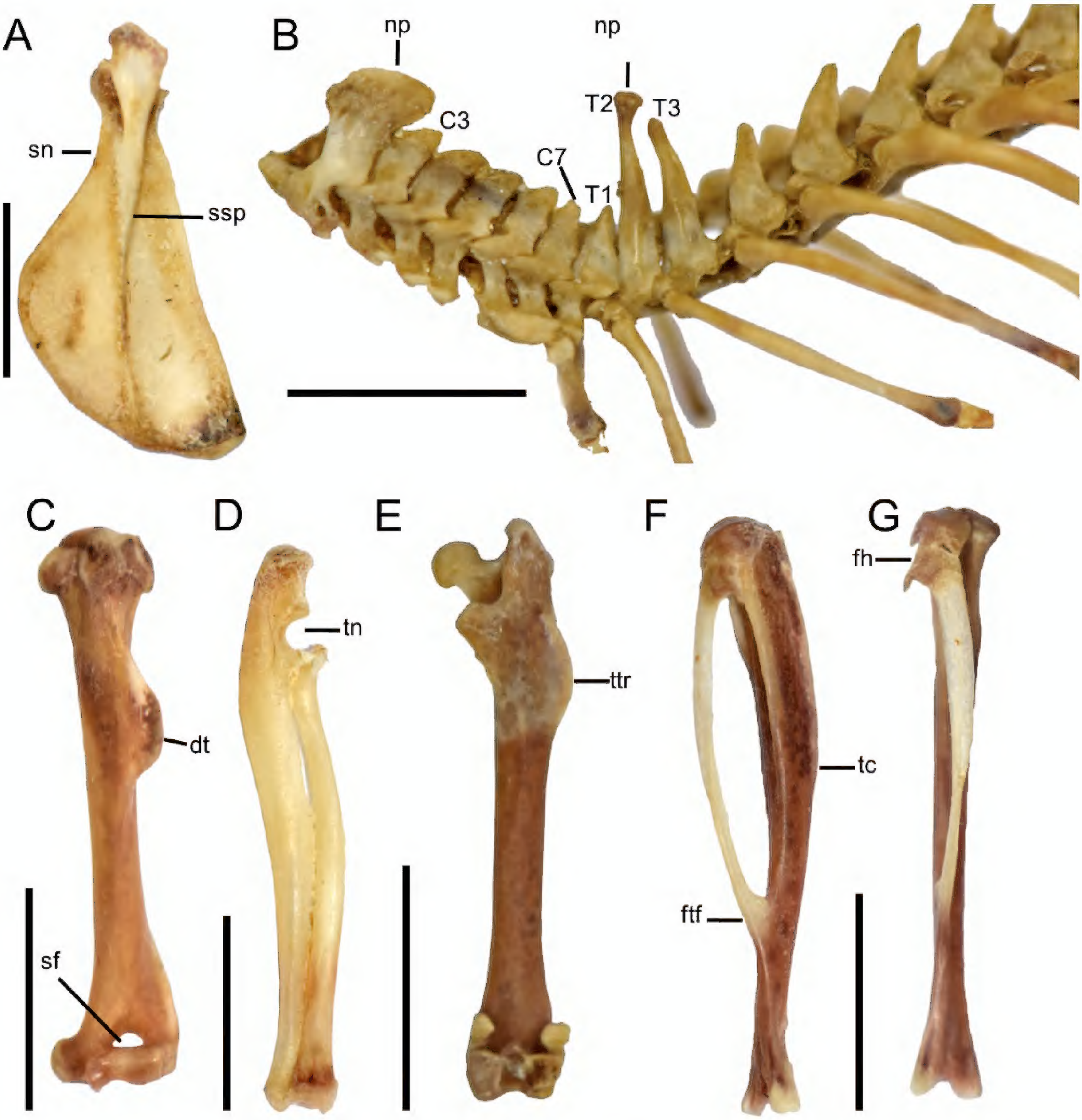

Figure 8. Lateral external view of the scapula (**A**), lateral view of the partial vertebral column including from axis to seventh thoracic vertebra (**B**), anterior view of humerus (**C**), medial view of radius-ulna (**D**), caudal view of the femur (**E**), lateral and caudal view of the tibia and fibula (**F** and **G**, respectively) of *Mindomys hammondi* (MECN 6228; Reserva Drácula, Carchi, Ecuador). Abbreviations: C3–C7, third to seventh cervical vertebrae; dt, deltoid tuberosity; ftf, fusion of tibia and fibula; fh, fibular head; np, neural process; sf, supratrochlear foramen; sn, scapular notch; ssp, scapular spine; tc, tibial crest; tn, trochlear notch; ttr, third trochanter; T1, T2 and T3, first, second and third thoracic vertebrae. Scale bars: 10 mm.

is separated from Reserva Drácula by about 132 kilometres and by the deep canyon formed by the Mira River (Fig. 9). At least for the recently described *Pattonimus*, the recognised species appear divided by the main river courses traversing the western montane forests in northern Ecuador and southern Colombia (Brito et al. 2020). A comparable scenario for *Mindomys* cannot be a priori discarded.

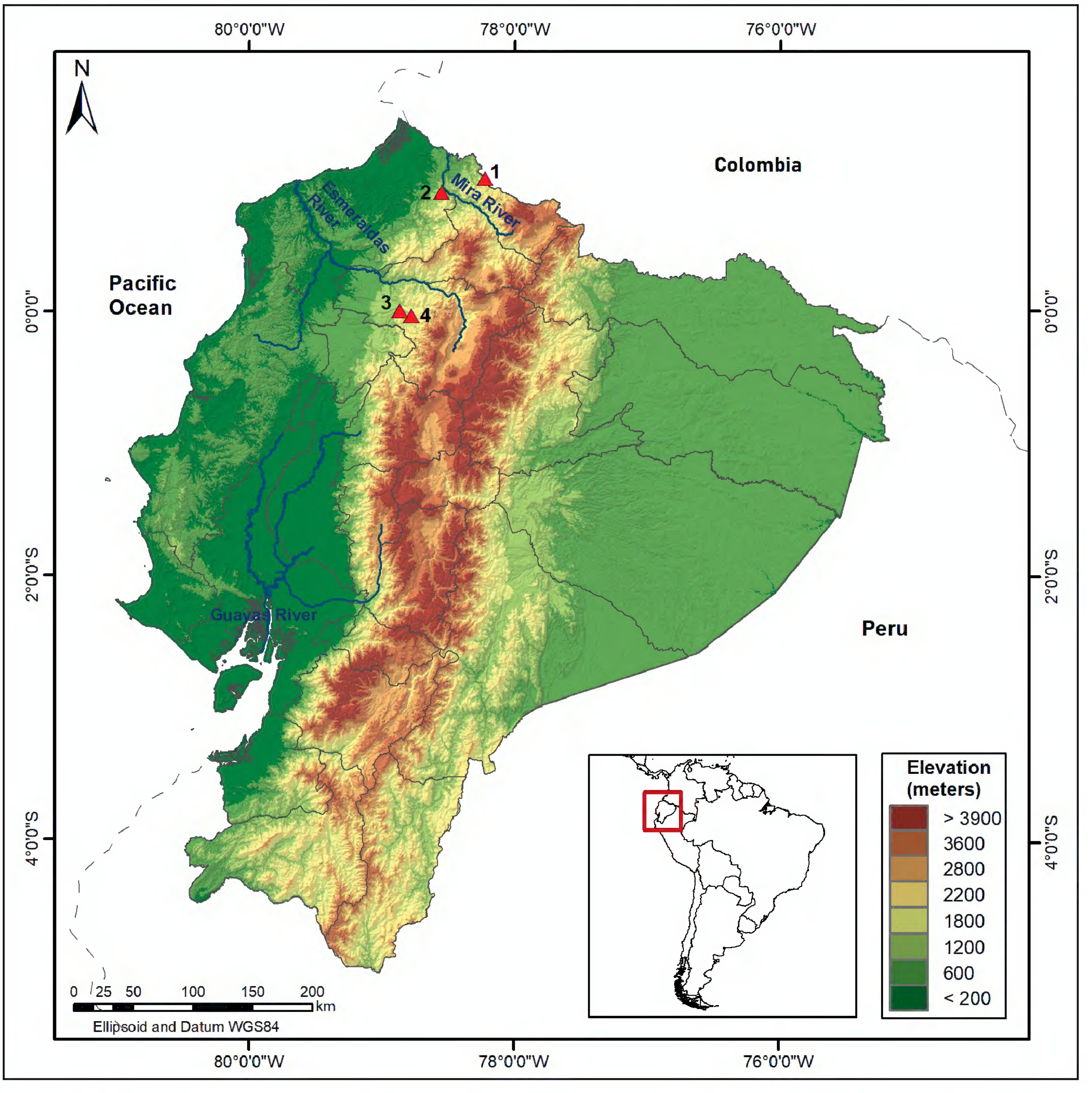

Figure 9. Known recorded localities for *Mindomys hammondi* (Ecuador): 1. Reserva Drácula (this note); 2. Alto Tambo, Esmeraldas (Pinto et al. 2018); 3. Saloya (probably the provenance of the specimen housed at the Museum of Comparative Zoology, Harvard, under the number MCZ 52688); 4. Mindo (type locality; Thomas 1913).

The phylogenetic position of *Mindomys* was recently explored, based on a combination of morphological and molecular traits and the genus was resolved as a member of the clade containing *Nephelomys* and *Pattonimus* (Brito et al. 2020). DNA was extracted from a muscle sample of the MECN 6228 using the Bilton and Jaarola (1996) protocol. The mitochondrial gene Cytochrome b (Cyt-b) was amplified, using primers MVZ 05 and MVZ 16H and the thermal profile of Smith and Patton (1993). A phylogenetic reconstruction under Maximum Likelihood (ML) was performed in the RAxML (Stamatakis 2014) programme; the GTR + G model was used for each of the partitions (1^{st}, 2^{nd} and 3^{rd} position). In addition, the genetic distance amongst MECN 6228, *M. hammondi* (a specimen from Esmeraldas, see

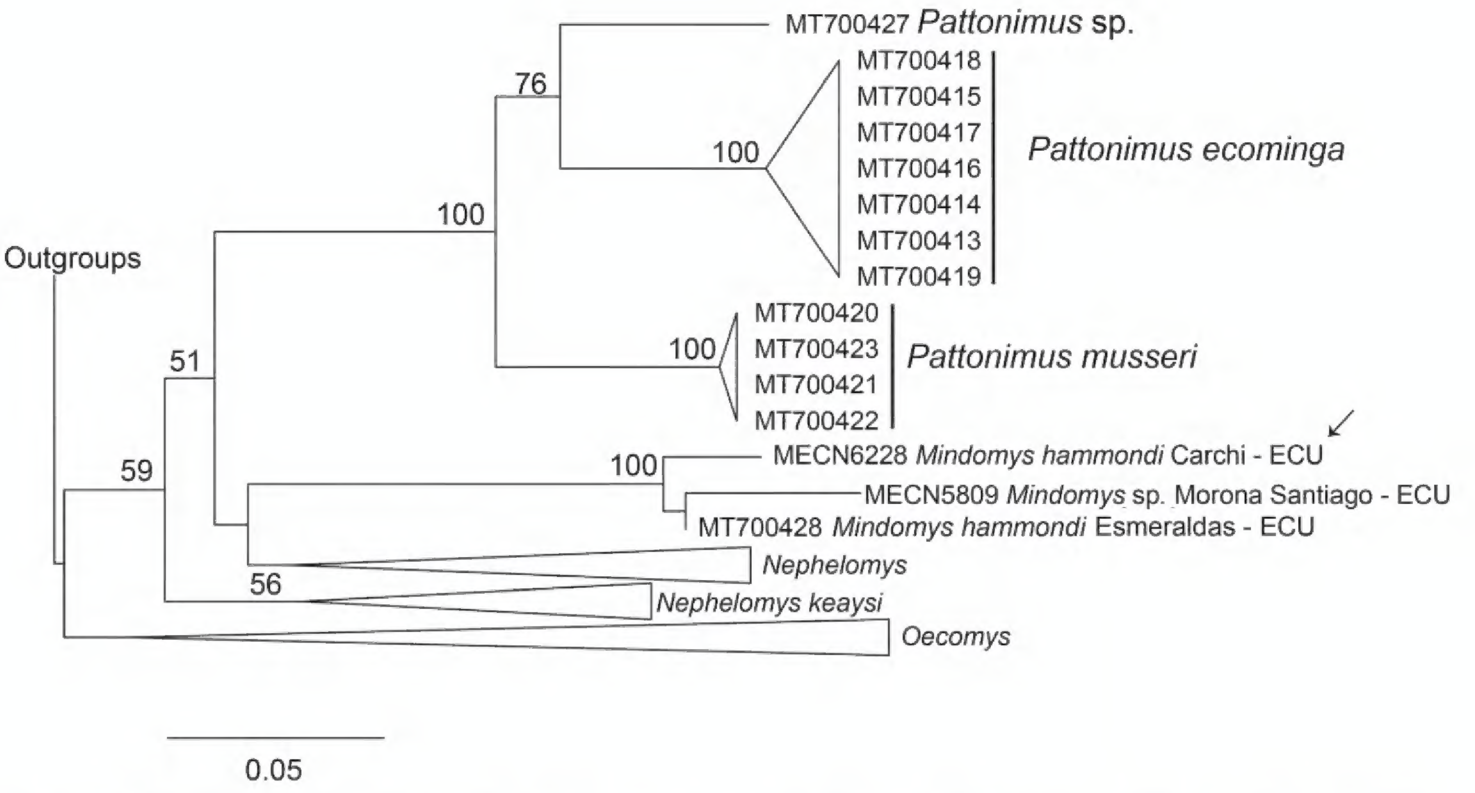

Figure 10. Maximum Likelihood phylogenetic tree, based on the mitochondrial gene Cyt b (800–1140 bp). Bootstrap values greater than 50 are shown. The arrow shows the position of the specimen of *Mindomys hammondi* (MECN 6228; Reserva Drácula, Carchi, Ecuador).

Brito et al. 2020) and *Mindomys* sp. (unpublished material from Cordillera de Kutukú) was calculated. The sequence of MECN 6228 was located as sister (BS = 100) to a clade including *M. hammondi* and *Mindomys* sp. (Fig. 10). The genetic distances between the studied samples ranged from 2.45% to 5.28%.

Mindomys, *Nephelomys* and *Pattonimus* share a variety of common anatomical traits and seem to represent an in-situ radiation mainly restricted to Andean cloud forests (Brito et al. 2020). However, the former departs from the others as the most specialised of this group to exploit an arboreal life condition. This is particularly reflected in the pes form and size as was early recognised by Hershkovitz (1944), but also in manus geometry as described above. Since the MECN 6228 was trapped on ground, some kind of cursorial activity is supported for this rat. In any case, the apparent scarcity of *Mindomys* probably mirrors its arboreal condition rather than actual rarity. Although *M. hammondi* was recently classified as Endangered (Roach and Naylor 2019), Data Deficient seems a more appropriate category because almost nothing is known about this cricetid.

The MECN 6228 is the first specimen of *Mindomys* to be added to any Ecuadorian mammal collection after more than a century since its original description. At the generic level within sigmodontines, *Megaoryzomys* and *Nesoryzomys* still lack specimens in local repositories. If a healthy exercise of sovereignty is the appropriation of biodiversity through knowledge, much remains to be done in Ecuador. This context highlights the necessity to deepen programmes of inventory and collection (Monfils et al. 2020), as well as to improve access of scholars to these resources.

Acknowledgements

Work at Reserva Drácula was undertaken with the field and logistic assistance of Karen Kuji (member of the "Minion" team) and the unrestricted support of Fundación EcoMinga and its current director, Javier Robayo. We want to highlight here Rainforest Trust and their "Species Legacy" programme, the Orchid Conservation Alliance, Reserva The Youth Land Trust, University of Basel and Fundación EcoMinga for their efforts to protect these montane forests. Callie Broaddus deserves the credit for the landscape photo in Figure 1A and Mateo Vega for Figure 9. Fernando Ayala (QCAZ) kindly collaborated with us by preparing the baculum represented in Figure 7D. Lou Jost generously read the manuscript and corrected the grammar and spelling; Luz Carrizo provides advice with postcranial description. To the mentioned persons and institutions, our deep gratitude. Field trips were approved by the Ministerio del Ambiente y Agua del Ecuador (permissions number No. MAAE-ARSFC-2020-0642). This note is a modest tribute to the memory of Analía Autino, Argentinean parasitologist who was a victim of Covid19.

References

Bilton DT, Jaarola M (1996) Isolation and purification of vertebrate DNAs. In: Clapp JP (Ed.) Species diagnostics protocols: PCR and other nucleic acid methods in molecular biology. Humana Press, Totowa, 25–37. https://doi.org/10.1385/0-89603-323-6:25

Björnhag G (1994) Adaptations in the large intestine allowing small animals to eat fibrous foods. In: Chivers D, Langer P (Eds) The digestive system in mammals (D. Chivers and P. Langer, eds). Cambridge University Press, Cambridge, 287–309. https://doi.org/10.1017/CBO9780511661716.018

Brito J, Koch C, Percequillo AR, Tinoco N, Weksler M, Pinto CM, Pardiñas UFJ (2020) A new genus of oryzomyine rodents (Cricetidae, Sigmodontinae) with three new species from montane cloud forests, western Andean cordillera of Colombia and Ecuador. PeerJ 8: e10247. https://doi.org/10.7717/peerj.10247

Brown JC (1973) The description of mammals. 1. The external characters of the head. Mammal Review 1(6): 151–168. https://doi.org/10.1111/j.1365-2907.1972.tb00333.x

Carleton MD (1973) A survey of gross stomach morphology in New World Cricetinae (Rodentia, Muroidea), with comments on functional interpretations. Miscellaneous Publications, Museum of Zoology. University of Michigan 146: 1–43.

Carleton MD (1980) Phylogenetic relationships in neotomine peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. Miscellaneous Publications, Museum of Zoology. University of Michigan 157: 1–146.

Chiquito EA, Percequillo AR (2016) On the rare species *Amphinectomys savamis* Malygin 1994 (Rodentia, Cricetidae, Sigmodontinae): New record and morphological considerations. Mammalia 81: 531–536. https://doi.org/10.1515/mammalia-2016-0101

Haidarliu S, Golomb D, Kleinfeld D, Ahissar E (2012) Dorsorostral snout muscles in the rat subserve coordinated movement for whisking and sniffing. The Anatomical Record 295(7): 1181–1191. https://doi.org/10.1002/ar.22501

Haidarliu S, Kleinfeld D, Ahissar E (2013) Mediation of muscular control of rhinarial motility in rats by the nasal cartilaginous skeleton. The Anatomical Record 296(12): 1821–1832. https://doi.org/10.1002/ar.22822

Hershkovitz P (1944) Systematic review of the Neotropical water rats of the genus *Nectomys* (Cricetinae). Miscellaneous Publications, Museum of Zoology. University of Michigan 58: 1–101.

Hill W, Osman C (1948) An undescribed structure in the rodent rhinarium. Nature 161(4086): 276–277. https://doi.org/10.1038/161276a0

Hooper ET, Musser GG (1964) The glans penis in Neotropical cricetines (family Muridae) with comments on classification of muroid rodents. Miscellaneous Publications, Museum of Zoology. University of Michigan 123: 1–57.

Monfils AK, Krimmel EL, Bates JM, Bauer JE, Belitz MW, Cahill BC, Caywood AM, Cobb NS, Colby JB, Ellis SA, Krejsa DM, Levine TD, Marsico TD, Mayfield-Meyer TJ, Miller-Camp JS, Nelson RMG, Phillips MA, Revelez MA, Roberts DR, Singer RA, Zaspel JM (2020) Regional collections are an essential component of biodiversity research infrastructure. BioScience 70: 1045–1047. https://doi.org/10.1093/biosci/biaa102

Percequillo AR (2015) Genus *Mindomys* Weksler, Percequillo and Voss. In: Patton JL, Pardiñas UFJ, D'Elía G (Eds) Mammals of South America. Vol. 2, 330–361.

Percequillo AR, Rodrigues do Prado J, Abreu EF, Dalapicolla J, Pavan AC, Chiquito EA, Brennand P, Steppan SJ, Lemmon AR, Lemmon EM, Wilkinson M (2021) Tempo and mode of evolution of oryzomyine rodents (Rodentia, Cricetidae, Sigmodontinae): A phylogenomic approach. Molecular Phylogenetics and Evolution 159: 107120. https://doi.org/10.1016/j.ympev.2021.107120

Pinto CM, Ojala-Barbour R, Brito J, Menchaca A, Carvalho AL, Weksler M, Amato G, Lee Jr TE (2018) Rodents of the eastern and western slopes of the Tropical Andes: Phylogenetic and taxonomic insights using DNA barcodes. Therya 9(1): 15–27. https://doi.org/10.12933/therya-18-430

Quay WB (1954) The anatomy of the diastemal palate in Microtine rodents. Miscellaneous Publications, Museum of Zoology, University of Michigan, 86: 1–41. [+ 4 plates]

Roach N, Naylor L (2019) *Mindomys hammondi*. The IUCN Red List of Threatened Species 2019: e.T15597A22330151. https://doi.org/10.2305/IUCN.UK.2019-1.RLTS.T15597A22330151.en

Smith MF, Patton JL (1993) The diversification of South American murid rodents: Evidence from mitochondrial DNA sequence data for the akodontine tribe. Biological Journal of the Linnean Society. Linnean Society of London 50(3): 149–177. https://doi.org/10.1111/j.1095-8312.1993.tb00924.x

Stamatakis A (2014) Raxml version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30(9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Thomas O (1913) New mammals from South America. Annals & Magazine of Natural History 12(72): 567–574. https://doi.org/10.1080/00222931308693443

Tirira DG, Azurduy Högström C (2011) Mamíferos ecuatorianos en museos de historia natural y colecciones científicas: 3. El Museo de Historia Natural de Gotemburgo (Suecia). Boletín Técnico 10, Serie Zoológica. Grupo de Biodiversidad IASA 7: 14–46.

Vorontsov NN (1967) Evolution of the alimentary system in myomorph rodents. Nauka Siberian Branch, Novosibirsk. [In Russian]

Vorontsov NN (1982) [The hamsters (Cricetidae) of the world fauna. Part 1. Morphology and Ecology]. Fauna of the USSR, New Series M° 125. Mammals 3: 1–452. [in Russian]

Voss RS (1988) Systematics and ecology of ichthyomyine rodents (Muroidea): Patterns of morphological evolution in a small adaptive radiation. Bulletin of the American Museum of Natural History 188: 262–493.

Voss RS, Carleton MD (1993) A new genus for *Hesperomys molitor* Winge and *Holochilus magnus* Hershkovitz, with comments on phylogenetic relationships and oryzomyine monophyly. American Museum Novitates 3085: 1–39.

Weksler M (2006) Phylogenetic relationships of oryzomine rodents (Muroidea: Sigmodontinae): separate and combined analyses of morphological and molecular data. Bulletin of the American Museum of Natural History 296: 1–149. https://doi.org/10.1206/0003-0090(2006)296[0001:PROORM]2.0.CO;2

Weksler M, Percequillo AR, Voss RS (2006) Ten new genera of oryzomyine rodents (Cricetidae: Sigmodontinae). American Museum Novitates 3537(1): 1–29. https://doi.org/10.1206/0003-0082(2006)3537[1:TNGOOR]2.0.CO;2

Appendix 1

External and craniodental measurements (provided in millimetres, except the body mass) of *Mindomys hammondi* (MECN 6228; Reserva Drácula, Carchi, Ecuador): head and body length = 175; tail length = 236 (the tip of the tail is cicatrised and, therefore, probably incomplete); hind foot length (including claw) = 42; ear length = 20; length of longest mystacial vibrissae = 78.74; length of longest superciliary vibrissae = 51.63; length of longest genal vibrissae = 29.90; body mass = 184 (in grams); occipitonasal length = 39.26; condylo-incisive length = 36.77; length of upper diastema = 10.77; crown length of maxillary toothrow = 6.5; length of incisive foramen = 5.65; breadth of incisive foramina = 2.52; breadth of M1 = 1.94; breadth of rostrum = 8.31; length of nasals = 13.80; length of palatal bridge = 8.68; breadth of bony palate = 3.83; least interorbital breadth = 6.48; zygomatic breadth = 19.63; breadth of zygomatic plate = 4.39; lambdoidal breadth = 15.48; orbital fossa length = 12.82; bular breadth = 4.80; length of mandible = 19.66; crown length of mandibular toothrow = 6.58; length of lower diastema = 4.64; length M1 = 3.06; width M1 = 1.94; length M2 = 2.20; width M2 = 1.95; length M3 = 1.51; width M3 = 1.68; length m1 = 2.68; width m1 = 1.88; length m2 = 1.96; width m2 = 1.88; length m3 = 2.05; width m3 = 1.65.